# EFFECTS OF DEFOLIATION ON REPRODUCTION OF A TOXIC RANGE PLANT, *ZIGADENUS PANICULATUS*

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ABSTRACT.— The effect of complete defoliation, prior to flower stalk appearance, on the reproductive success of foothill deathcamas, a toxic range plant, was studied in northern Utah. Defoliated plants did not replace their leaves. Defoliation had no effect on total number of flower stalks produced but did significantly slow the rate of stalk emergence and reduce the number of plants that produced open flowers. The number of leaves produced by control plants was also positively associated with the probability of producing a flowering stalk. Few plants in either defoliated or control treatments set seed, probably because of inactivity of pollinators during a cold and wet spring. It is suggested that species, such as deathcamas, which either produce leaves early in spring or are liliaceous geophytes, may be especially vulnerable to herbivory.

Among the characteristics thought to render plant species "apparent," or relatively easy for herbivores to find, are the perennial habit and large size, both of individuals and of populations (Feeney 1976, Rhoades and Cates 1976, Rhoades 1979). Apparent species are also hypothesized to reduce their susceptibility to herbivory by diverting relatively large amounts of energy from vegetative and reproductive functions to the production of antiherbivore compounds.

Foothill deathcamas (*Zigadenus paniculatus* [Nutt] S. Wats; Liliaceae) is a bulb-forming range plant of the western U.S. (James et al. 1980) that possesses some of these characteristics of apparency: it is perennial and is commonly found in large numbers throughout its range, although individual plants are small. Apparency is further increased because deathcamas is among the first species to produce leaves in the spring (James et al. 1980, pers. obs.): it is therefore extremely attractive to mammalian herbivores that have subsisted on low-quality forage through the winter. Despite their availability, few plants ($\approx$ 10.0 percent) display any evidence of herbivory (Tepedino, unpubl. ms.), evidently because of the numerous steroid alkaloids present in the leaves and other plant parts (Willaman and Li 1970) that are toxic to mammals (Marsh and Clawson 1922).

In addition to the apparently large commitment to the defense of leaf tissue by the production of alkaloids, there are other reasons for suspecting deathcamas to be particularly vulnerable to herbivory when it occurs. Although most perennials typically replace their leaves soon after defoliation (Jameson 1963, Kulman 1971, Rockwood 1974), evidence suggests that geophytic species of the Liliales may be incapable of doing so (Heath and Holdsworth 1948); under normal conditions, once the presumptive flower stalk bud is formed in early spring no further leaf initials are cut. Also, a minimum number of leaves has been shown to be necessary for flower stalk production for several liliaceous species (Heath and Holdsworth 1948 and references therein). Thus, defoliation of deathcamas may significantly impair reproductive success by lowering the number of flowers or seeds produced. The relationship between the number of leaves and flowers produced and the effect of artificial defoliation on reproductive success are reported here.

## METHODS

The study site (alt. 1400m) was at the top of a west-facing embankment, 8 km south of Avon, Utah (Cache Co.), along County Road 165. Here numerous deathcamas plants grew among sagebrush (*Artemisia* sp.) and associated forbs.

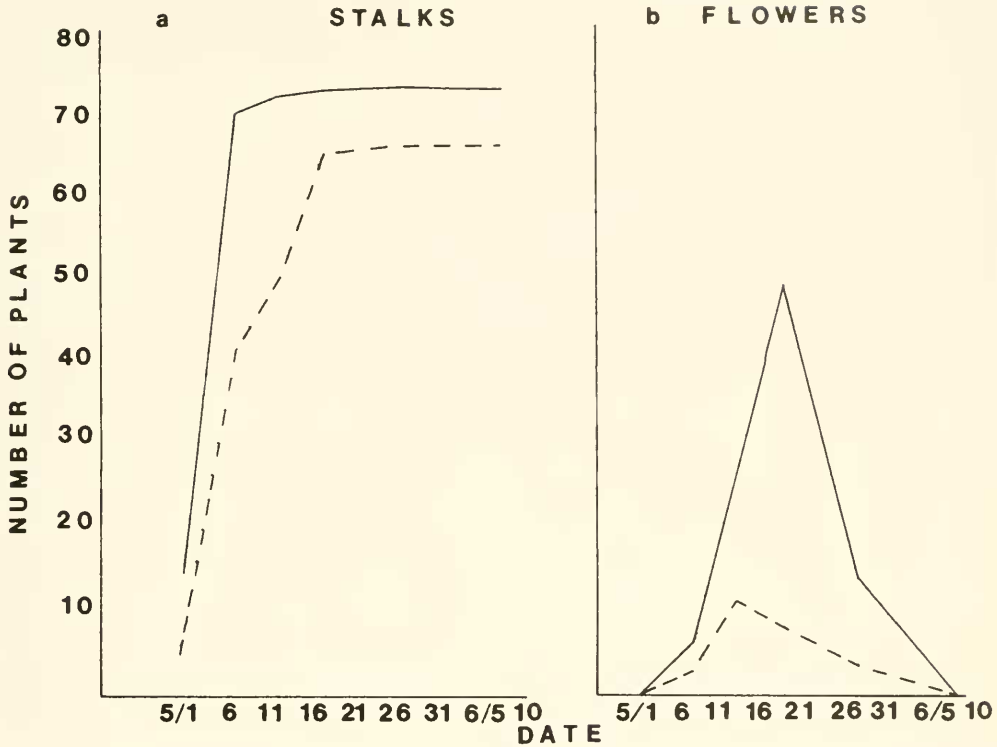[1]USDA-ARS-WR, Bee Biology and Systematics Laboratory, Utah State University, UMC 53, Logan, Utah 84322.

Fig. 1. Number of plants producing a, flowering stalks; b, open flowers for defoliation (dashed line); and control (solid line) treatments.

Foothill deathcamas produces 3–9 basal leaves from a tunicate bulb in early spring, followed by a single paniculate flowering stalk 4–6 weeks later. Plants with 5 or more leaves were completely defoliated on 23 April 1981 after the basal leaves were fully extended, but before appearance of the flowering stalk. Leaves of 100 plants were counted and removed at soil level with a razor blade. At the same time, a plant nearby (between 1–2 m) each of those treated was selected as a control. Leaves of controls were also counted. All plants were marked with plastic labels.

Plants were subsequently examined at approximately weekly intervals for developmental stage of the flowering stalk. Absence or presence of the stalk, presence of open or spent flowers, and fruit maturation (judged by expansion of the perianth) were recorded.

Precipitation and temperature records were obtained from a Utah State University weather station located 19 km north of the site at similar elevation.

## RESULTS

Unlike some other perennial species, Z. paniculatus did not replace lost leaf tissue; once defoliated, experimental plants remained in that condition for the rest of the growing season.

Flowering stalks of plants from both treatments had begun to emerge by the first examination date (1 May). However, the rate of emergence was slower for defoliated plants than for controls (Fig. 1a); a chi-square test of equal distribution of plants with flowering stalks in each treatment was significant for the first three sampling dates (1 May, $X^2 =$ 3.86, P = 0.05; 7 May, $X^2 = 7.58$, P<0.01; 12 May, $X^2 = 3.97$, P = 0.05). Although flowering stalks of defoliated plants emerged more slowly, by the end of the flowering season there was no significant difference between treatments in the total number of stalks produced ($X^2 = 0.35$, P<0.50).

The major difference between defoliated and control plants was in the number of flowering stalks that produced open flowers

(Fig. 1b). Only 21 of the 66 stalks produced by defoliated plants developed open flowers as compared to 59 of 71 control stalks. (Two additional control stalks were decapitated by herbivores before they flowered). Flower buds on most stalks of defoliated plants withered soon after the stalks emerged, and stalks subsequently turned brown.

Few plants of either treatment set seeds. Only one defoliated plant, and five control plants produced seeds. Lack of seed set by control plants was probably due to inactivity of pollinators caused by cold and rainy weather. Precipitation fell on 15 of 31 days in May and the maximum temperature was below 21 C (70 F) on 18 days. Only 7 days were both rainfree with maximum temperature at or above 21 C, and all these came at the beginning or end of the month (days 1, 2, 25, 28–31).

The number of leaves produced by a plant was associated with stalk production for both treatments. Table 1 shows the distribution of plants by leaf number categories; the overall distribution did not differ significantly between treatments ($X^2$ = 1.38, d.f. = 3; in this and the following analysis leaf number categories have been combined when expected values were <5.0, Maxwell [1961]). For each treatment the proportion of plants producing stalks increased with leaf number (Table 1). A comparison of the number of plants in each leaf category that produced stalks with those that did not was significant for both treatments (defoliated, $X^2$ = 7.2, d.f. = 2, P<0.05; control, $X^2$ = 12.2, d.f. = 1, P<0.001): plants with more leaves had a greater probability of producing a stalk even when leaves had been removed. A comparison between treatments of the distribution of plants with stalks by leaf number showed no significant difference ($X^2$ = 0.06, d.f. = 2, P<0.50).

Plants with more leaves also exhibited a greater tendency to produce open flowers (Table 1). However, when plants producing flowers were compared by leaf number with plants producing only stalks, differences between treatments were apparent. For control plants the distributions did not differ significantly ($X^2$ = 0.96, d.f. = 1); if a plant sent up a stalk, there was a high probability (80.8

percent) that flowers would open, irrespective of leaf number. For defoliated plants there was a greater probability for plants that had produced more leaves to produce some open flowers on the stalk than for those with fewer leaves ($X^2$ = 3.36, d.f. = 1, P = 0.07).

## DISCUSSION

Defoliation had irreparable effects on the reproductive potential of Z. paniculatus. Although removal of leaves just before stalk emergence did not affect the likelihood of producing a stalk, it did significantly delay the emergence of stalks and reduce the probability that any flower buds would reach anthesis. These results are in general agreement with other studies that have shown that simulated herbivory can significantly reduce numbers of flowers (Blaisdell and Pechanec 1949, Callan 1949, Simmonds 1951, Mueggler 1967, Enyi 1975) or seeds (Sackston 1959, Rockwood 1974, Enyi 1975), and also delay flowering (Collins and Aitken 1970) (see Jameson 1963, Kulman 1971 for reviews).

The effects of defoliating deathcamas, however, may be more profound than the simple elimination of a single year's reproduction. The results suggest that stored carbohydrates from the previous year are depleted in the production of leaves. Leaves, in turn, hasten emergence of the stalk, and are required for maturation of flowers, seeds, and the synthesis of storage material for the subsequent year's vegetative growth. But, unlike many other perennials, Z. paniculatus is apparently unable to produce a second crop of leaves after defoliation. If leaves are cropped

TABLE 1. Distribution of defoliated and control plants by number of leaves/plant, and the percentage of total plants in each category that produced flowering stalks and open flowers.

| | Number of leaves | | | | |
|---|---|---|---|---|---|
| | 5 | 6 | 7 | 8 | 9 |
| Defoliated | | | | | |
| Total no. | 0 | 13 | 53 | 29 | 5 |
| With stalk (%) | 0.0 | 38.5 | 64.2 | 75.9 | 100.0 |
| With flowers (%) | 0.0 | 15.4 | 13.2 | 34.5 | 40.0 |
| Control | | | | | |
| Total no. | 2 | 8 | 60 | 24 | 6 |
| With stalk (%) | 0.0 | 25.0 | 70.0 | 95.8 | 100.0 |
| With flowers (%) | 0.0 | 25.0 | 53.3 | 83.3 | 83.3 |

before stalk emergence, plants may have had insufficient photosynthetic surface to produce storage material for the following year. Thus, it is possible that a single defoliation episode is sufficient to cause either death of the plant or to eliminate reproduction for more than one year. If this proves to be the case, the production of antiherbivore compounds becomes important.

The positive relationship between the number of leaves produced and the likelihood of sending up a flowering stalk has also been reported for other species in the Liliales (Heath and Holdsworth 1948). These results suggest that the number of leaves produced increases with age of the plant, and that plants do not begin flowering until the second or third year. This assertion needs more careful examination; however, numerous plants with 3–5 leaves in a population at higher altitude (1850 m) have been observed both to bloom and produce seeds (Tepedino, unpubl. ms.).

Schemske et al. (1978) showed that seed production in self-incompatible spring-flowering herbs can vary considerably from year-to-year, and suggested that this variation was due to the effect of unpredictable spring weather on pollinators. A similar explanation seems appropriate for Z. paniculatus, which also requires insects for pollination (Tepedino 1981). Few plants in the control treatment set seed, and this was associated with an absence of pollinators during an extended period of cold and wet weather. Conversely, in the previous year, when weather was more conducive to insect activity, most plants set seed at a nearby site (pers. obs.).

Two characteristics of the growing season and life form of Z. paniculatus suggest possible modifications of the concept of plant apparency. First, as noted above, plant species that leaf out early in spring are extremely apparent to mammalian herbivores, and we should expect the leaves of such plants to be well defended. This seasonality component of apparency seems to have been previously ignored. A cursory perusal of James et al. (1980) suggests that 75–80 percent of the plants most poisonous to livestock in the western U.S. begin growth in early spring, so the idea would seem to deserve further attention.

Second, several workers have noted that, among the monocots, only the Liliales are well represented in the number of species that produce alkaloids (Hegnauer 1966, Levin and York 1978). Tomlinson (1980) has pointed out that many of these species are geophytes. Perhaps the leaves of many of these species are irreplaceable, as in deathcamas and other liliaceous species (Heath and Holdsworth 1948), and must therefore be heavily defended against herbivory.

## Literature Cited

Blaisdell, J. P., and J. P. Pechanec. 1949. Effects of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. Ecology 30:298–305.

Callan, E. M. 1949. Effect of defoliation on reproduction of Cordia macrostachya. Bull. Entomol. Res. 39:213–15.

Collins, W. J., and Y. Aitken. 1970. The effect of leaf removal on flowering time in subterranean clover. Aust. J. Agric. Res. 21:893–903.

Enyi, B. A. C. 1975. Effects of defoliation on growth and yield in groundnut (Arachis hypogea), cowpeas (Vigna unquiculata), soybean (Glycine max), and green gram (Vigna aurens). Ann. Appl. Biol. 79:55–66.

Feeny, P. 1976. Plant apparency and chemical defense. Rec. Adv. Phytochemistry 10:1–40.

Heath, O. V. S., and M. Holdsworth. 1948. Morphogenic factors as exemplified by the onion plant. Sym. Soc. Exp. Biol. 2:326–350.

Hegnauer, R. 1966. Comparative phytochemistry of alkaloids. Pages 211–230 in T. Swain, ed., Comparative phytochemistry. Academic Press, New York.

James, L. F., R. F. Keeler, A. E. Johnson, M. C. Williams, E. H. Cronin, and J. D. Olsen. 1980. Plants poisonous to livestock in the western states. USDA Agric. Infor. Bull. 415. 90 pp.

Jameson, D. A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532–594.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol. 16:289–324.

Levin, D. A., and B. M. York, Jr. 1978. The toxicity of plant alkaloids: an ecogeographic perspective. Biochem. Syst. Ecol. 6:61–76.

MARSH, C. D., AND A. B. CLAWSON. 1922. The death-camas species, *Zygadenus paniculatus* and *Z. elegans*, as poisonous plants. USDA Bull. No. 1012. 25 pp.

MAXWELL, A. E. 1961. Analysing qualitative data. Methuen, London.

MUEGGLER, W. F. 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48:942–949.

RHOADES, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3–54 *in* G. A. Rosenthal and D. H. Janzen, eds., Herbivores: their interaction with secondary plant metabolites, Academic Press, New York.

RHOADES, D. F., AND R. G. CATES. 1976. Toward a general theory of plant antiherbivore chemistry. Rec. Adv. Phytochemistry 10:168–213.

ROCKWOOD, L. L. 1974. The effect of defoliation on seed production of six Costa Rican tree species. Ecology 54:1363–1369.

SACKSTON, W. E. 1959. Effects of defoliation on sunflowers. Can. J. Plant Sci. 39:108–118.

SCHEMSKE, D. W., M. F. WILLSON, M. N. MELAMPY, L. J. MILLER, L. VERNER, K. M. SCHEMSKE, AND L. B. BEST. 1978. Flowering ecology of some spring woodland herbs. Ecology 59:351–66.

SIMMONDS, F. J. 1951. Further effects of the defoliation of *Cordia macrostachya* (Jacq.) R. and S. Canadian Entomol. 83:24–27.

TEPEDINO, V. J. 1981. Notes on the reproductive biology of *Zigadenus paniculatus*, a toxic range plant. Great Basin Nat. 41:427–430.

TOMLINSON, P. B. 1980. Monocotyledonous habit in relation to morphology and anatomy. Sym. Linn. Soc. London 8:7–19.

WILLAMAN, J. J., AND H. L. LI. 1970. Alkaloid-bearing plants and their contained alkaloids. Lloydia (supplement) 33 (3A). 286 pp.